Modeling Resource Competition[1]

Ethology & Behavioral Ecology

Introduction: First, let's start with a definition of COMPETITION. For our purposes (since this is a behavior course) it is the influences of individuals on each other's behavior when some resource is limited. Limitation of resources implies that there is less resource available than individuals could use and turn into reproduction. Thus, resources are first limited and competition will first occur even when there are far more resources than are required for an individual to get by. On the other hand, resources can also be so abundant that no individual could possibly utilize them fully. In cases like this, animals do not generally compete (although competition might still occur if individuals decided to try to obtain the same subset of the total amount of available resource).

There are two general types of competition that we will consider:

- **EXPLOITATION COMPETITION**: In this form the animals will find a way to use the resource without fighting over it. By contrast,
- **INTERFERENCE COMPETITION** implies that resources are partitioned among individuals through some sort of aggressive behavior that reduces the ability of others to exploit a resource, usually this is termed **RESOURCE DEFENSE**

Let's take these in turn and then look at an example.

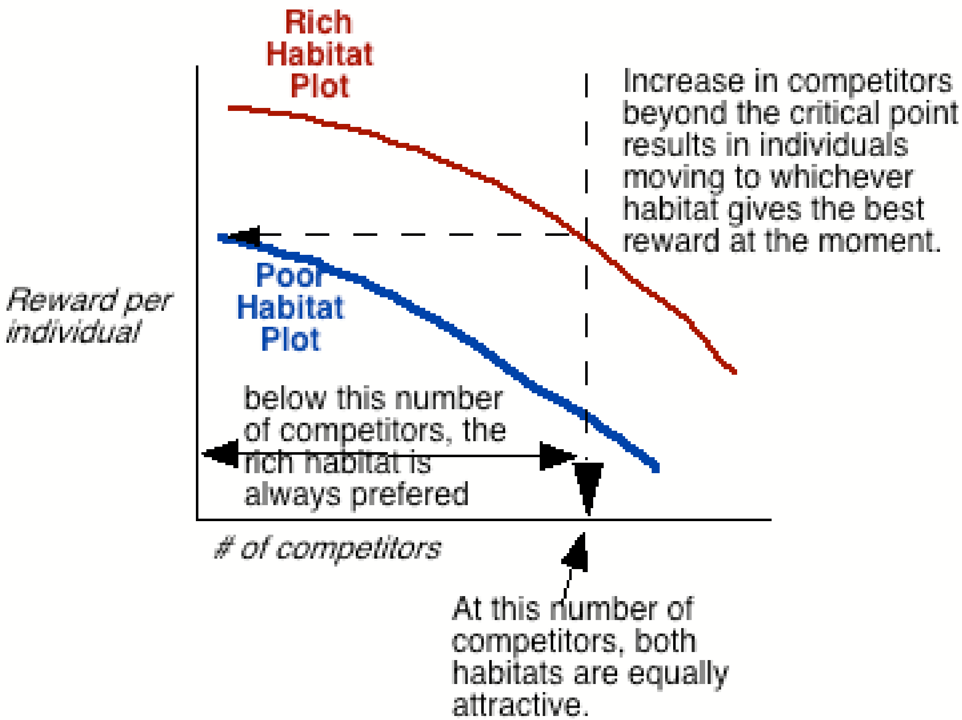
EXPLOITATION COMPETITION:

1. **Scramble Competition** -- simply grab what you can without interfering or intimidating other competitors. The organisms that are best at obtaining the resource (without fighting etc.) are the most successful.

2. A rather different model implies that all individuals are equally good competitors and they do not fight. In this idyllic model, individuals distribute themselves so that the rewards are equal. It is called an **IDEAL FREE DISTRIBUTION.** Let's look at the theoretical model as proposed by Fretwell (1972, *Populations in a Seasonal Environment*, Princeton Univ. Press)

   1. Assume two habitats; one is better than the other
   2. First animals faces a choice, it will go to better one as shown on the next page
   3. This degrades value of better of the better habitat (see graph)
   4. As density increases, better becomes less better
   5. Eventually the poor becomes equal in reward to the degraded and no longer "good" habitat; animals start to exploit it.
   6. Things will pretty much go back and forth from now on with the result being that everyone gets the same rewards.

[1] Prepared with heavy reliance on Krebs and Davies, Ch. 5. "Competing for Resources", *An Introduction to Behavioural Ecology* Third Ed. 1993 Blackwell



A famous experimental example of a possible ideal free distribution:
Milinski (1987, in *Foraging Behavior* ed. Kamil and Krebs; H.R. Pulliam pub): stickleback fish of the same size and presumably of the same competitive abilities. The idea is to see where the fish go when prey (a small freshwater shrimp-like organism, *Daphnia*) are introduced at different rates at each end with the result that a good and bad habitat are created.
Example:
Food reward at each end is simply the number of items (or some equivalent measure) -- **b** -- divided by the number of foragers (**n**):

eq. 1 reward/individual = b / n

Now, in an ideal free distribution, the rewards to everyone must be the same. Thus:

eq. 2 benefit per individual at end #1 = benefit/indiv at #2

Now suppose that **k** is some factor that weighs the relative amounts of food given on the "starting" side of the tank relative to the other side (*i.e.*, the relative amount of food in one patch compared to the other patch). Thus, if there is twice as much food on the reference (start) patch, k = 2; if half as much, k = 0.5.
Now, lets assume that initially all of the fish are at the reference end. We now start adding food to each end. What will be the equilibrium mix of fish?

- Let **n** equal the total number of fish at the starting end and

- **x** is the number that leave.
- Thus, the starting side (which has most fish at first) will end up with n-x fish

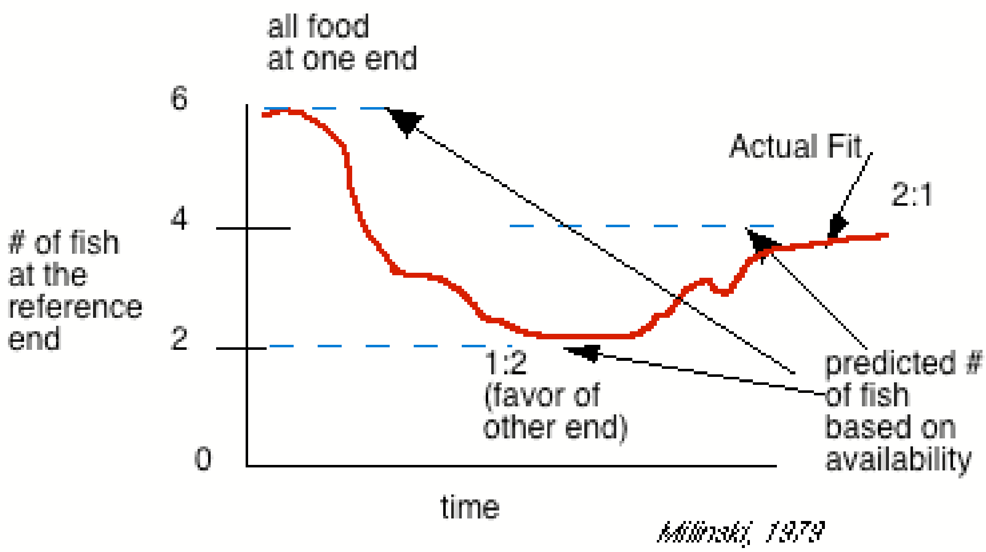
So, we have the following if we have an ideal free distribution:

eq. 3a $k*b / (n-x) = b / (x)$
3b $k * x = n - x$
3c $kx + x = n$

Let's get a numerical prediction. Let's suppose that the "reference" side is twice as rich as the other patch. Let's also assume we have 6 identical fish. Then:

eq. 4a $kx + x = n$
4b $2x + x = 6$
4c $x = 2$

Therefore there will be four fish at the rich end and two at the poor end.
When Milinski did the actual experiment he found the following:

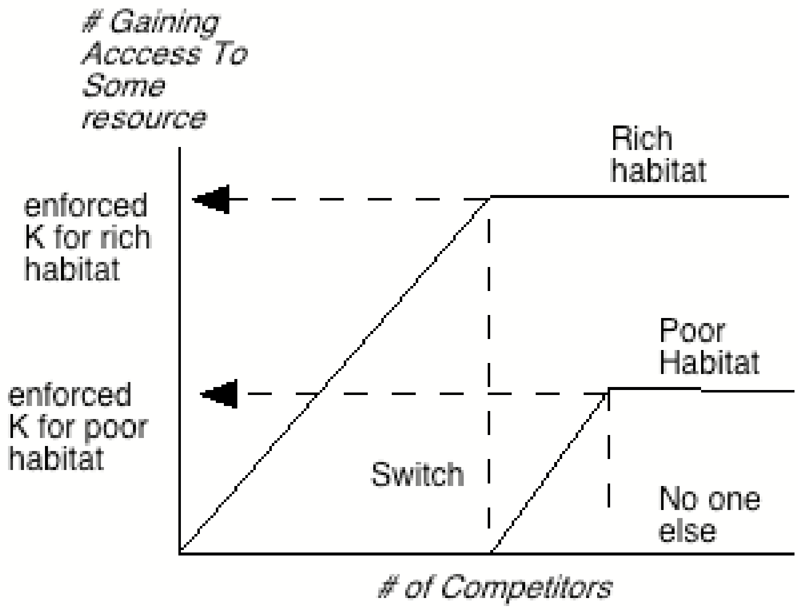


INTERFERENCE COMPETITION **The Resource Defense Model:**
(Brown 1969, Am Nat. 103: 347).
Imagine two habitats, one rich, one poor.
First, some definitions
Home range the area typically visited by an animal on a regular basis.
Core -- most heavily used part of the home range, often reserved for its more or less exclusive use
TERRITORIES: areas containing resources that are occupied more or less exclusively by one animal or a group. Others are excluded by aggression or

display. -- defended core areas.

Territories, cores, home ranges etc. can apply to single individuals or any sort of social grouping. Humans and other primates clearly have territories owned by both individuals and in other cases by groups; frequently these are savagely defended. The same is true of many other animals.

Jerrum Brown's model of what happens with two habitats:



Notice that each habitat has a maximum number of individuals that can be present. This number is decided by the individuals themselves. Thus, although it has some analogy to carrying capacity, it is not a true K.
<u>Unlike ideal free distributions, territories are not significantly degraded by additional animals. This is because the additional animals do not gain access to the resource. One individual, the despot, takes all the resources (or just about all) and excludes the others,</u>

Warning: the above formulation is idealistic -- in fact, costs of maintaining territories when there are more competitors around can lower their value as we will see when we get to economic defense models, below.

Notice what happens is that the first habitat fills then the second one; note also that the second one never fills with as many individuals -- after all, it's not as good!

Those who don't obtain territories are termed <u>FLOATERS</u> and other <u>EXCLUDED INDIVIDUALS.</u> Floaters typically try to gain territories or exploit those of others at

the margin; excluded individuals may simply give up and go try to do something else (like fatten up for next year).
One convincing way to show resource defense is through removal experiments; when owners are removed, the territories are quickly occupied either by swaps or by floaters coming in.

III. An Example of Resource Competition

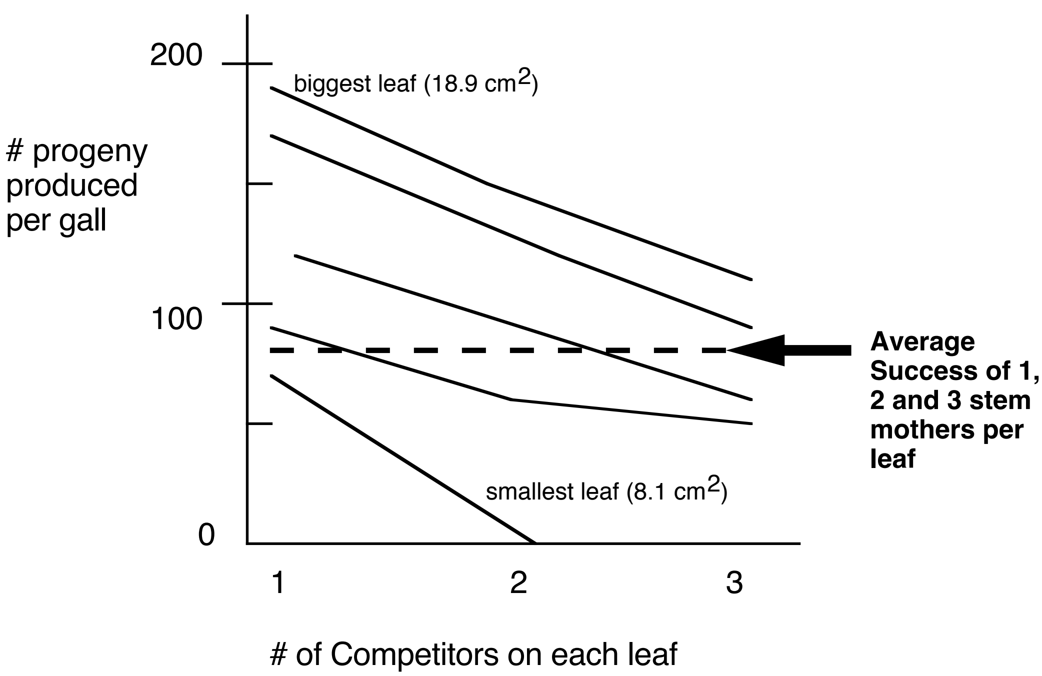
Poplar Leaf Aphids (hemiptera -- small relatives of cicadas)-- these are small insects whose young resemble small adult. When eggs are laid, the young hatch inside the leaf. The result is that the plant tries to wall them off by producing a **gall** -- a swelling of tissue around the nymph (larva).

Whitman measured the reproductive success of leaf poplar aphids as a function of leaf size (patch richness -- bigger leaves produce more juice), number of competitors on a leaf, and finally position of the gall on a leaf.
The first thing he noticed was that **larger leaves are occupied first** --

- *all large leaves are occupied (2% of total)*
- *the 33% of smallest leaves were avoided*.

Moreover, Whitman showed that females on larger leaves produced more progeny (by parthenogenesis -- we'll discuss this a bit later in the course). Thus, females were selecting the best habitat and they moved down to poorer habitat only when there were many competitors.
But **was it resource defense or ideal free distribution**? Here are his data:

Reprod. Success of Poplar Aphids on Leaves of Different Richness (size) and with Different #s of Competitors



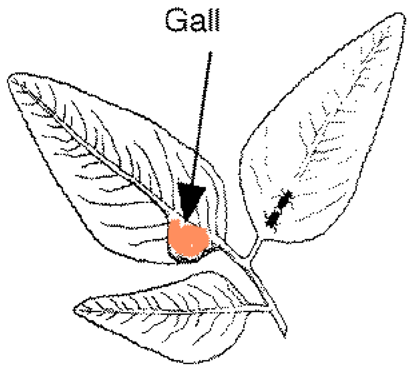
Conclusions from this graph:

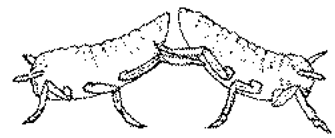
1. At any competitor density, success increases with habitat quality.
2. Within a habitat (leaf), success decreases with number of competitors.
3. If all the AVERAGE SUCCESS PER LEAF SIZE CLASS is compared for leaves with 1, 2 and 3 competitors, there are **no significant differences** in success
4. Nor were there differences per leaf with respect to other fitness measurements such as
   - abortion rate
   - development rate
   - predation rate

These data might be mistakenly taken as evidence that an ideal free distribution is operating. After all, a major condition for an ideal free distribution is that average rewards are everywhere the same. Even though some leaves are better than others, by this model, increased density simply implies that everyone has less and therefore everyone does less well, (review the ideal free distribution model).

HOWEVER:, Whitman looked closer and noticed that ON EACH LEAF, there was a difference in success depending on where on the leaf the aphids were located. The stem mother who laid her eggs <u>nearest the main vein's origin consistently did the best on the leaf</u>. Thus, average success is not the best metric of what is happening -- it merely says that a total resource tends to be partitioned about the same in all habitats.

The observation of a spatial effect on a leaf implied that there were favored positions. Moreover, Whitham had also noticed that resource defense was involved. As predicted from the defense model, **removal of a female from a favored position (before she has laid her eggs, while she is feeding) results in another taking over**. Also, the leaf mothers tend to sort things out among themselves by fighting -- typically they kick each other. These fights sometime result in the death of one of the combatants.





Stem Mother
Aphids
Kick Fighting

The presence of these kick fights and the results of removal of the basal stem mother both suggest that **on any given leaf some sort of interference competition is occurring** and the victors are getting what is considered the most desirable part of the leaf. (The figure above was taken from Alcock, Animal Behaviour, and 3rd edition).

Sticklebacks: males are undoubtedly different in competitive ability. Thus, the way the subordinates distribute themselves in relation to the despots could also produce a distribution that might appear to correspond with an ideal free distribution. Think about how this would happen.

IV. How large should a territory be?

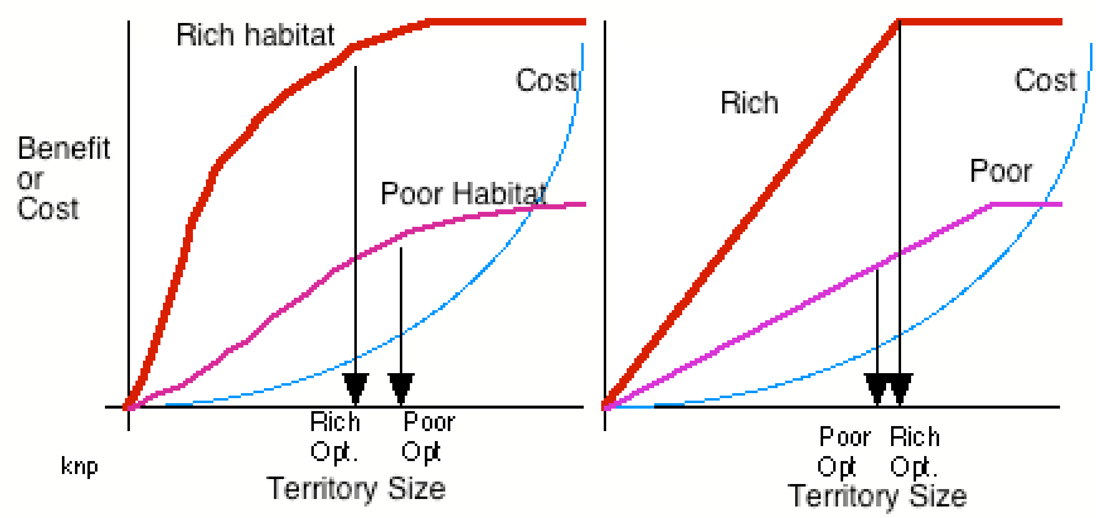
There have been a number of attempts to describe how large a territory should be. McNab and others have proposed somewhat simplistic models that equate territory size with the animal's resting metabolic rate (McNab, B. K. 1963. Bioenergetics and determinants of home range size. *American Naturalist* 97:133–140). These models all assume that territories are for the purpose of meeting energy demand and since food is obtained over some area of habitat that animals with higher total daily energy demands will, when all else is equal, require larger territories or home ranges.

In fact, energy must be an important consideration. For instance, a recent detailed analysis by Gad and Garland (2002, Lizard home ranges revisited: the effects of sex, body size, diet, habitat and phylogeny, Ecology 83:1870-1885) revealed that body size and therefore metabolic rate was a very important determinant of home range size. However, it also found differences related to sex and mating system, the habitat where the lizards lived, and the foods they ate. So, hypotheses just based on energy requirements are useful but often very incomplete since they ignore all factors of habitat richness, the allocation of time to various activities (for instance, searching for a mate) etc.

A territory makes no sense unless it results in an economic or some other gain for the holder. Territories can be costly to hold and even the richest situations eventually are too costly. So, can we model territory size? The best approach is an optimality model.

However, we need to be careful. Let's start out with a warning that illustrates how important it is to know the correct shapes of the costs and benefit curves. On the next page are two optimality models constructed by Tom Schoener. In each case benefit or cost are measured by some fitness related currency and the decision variable is territory size. They differ in the ways benefits increase with size and as a result end up coming to two very different conclusions about the relative sizes of territories in rich and poor habitats.

Resource Defense Models (Schoener 1983, *Am Nat.* 121:608)



You should be able to justify both of these approaches; there are almost certainly conditions that are appropriate for each model. You should be able to explain the positioning of each line, the slopes, etc, and you should be able to give conditions that would change the slope, peak and relative values of each graph. You might even be able to imagine other reasonable scenarios -- see what types of result they give.

V. The Economics of Territorial Defense -- When Should Animals Defend Territories?

The economics of territorial defense have been dealt with by many behavioral ecologists. Many look at territorial defense in terms of benefits associated with territoriality as compared to the costs. The reasonable assumption is that for territorial defense to occur, B > C. We will examine in detail a classic study that takes this approach.

In 1975 Gill and Wolf published "Economics of feeding territoriality in the golden-winged sunbird" (Ecology 56: 333 - 345). Theirs is a relatively straightforward but hardly simple model that attempts to answer the question of when an animal should switch from being territorial to non-territorial. It is assumed that the variable of interest with respect to this switch is the daily energy balance -- is the animal's energy budget in balance or surplus or is the animal relying to some degree on stored energy? We will soon see that Gill and Wolf selected animals incapable of being in negative energy balance for more than a few days. Thus, they were ideal subjects for testing the idea that territoriality is subject to its energetic consequences.

Sunbirds are an African equivalent to the New World's hummingbirds. Like hummingbirds, they are nectivores. Thus they obtain most of their calories from the sweet nectar of flowers (nectar is commonly up to 40% sugars). By way of note (not germane to this problem but of general interest), hummingbirds and sunbirds must both also obtain protein. They normally get it from feeding on insects. Also, there is a lot of **co-evolution** between these types of birds and the flowers they visit. The birds have long bills that allow them to probe deep into the flowers for nectar. The flowers themselves have long corollas that require long beaks (making them unsuitable for insects which simply cannot reach the nectar); moreover, they tend to be colored red or orange which birds seen especially well (perhaps an example of "sensory exploitation" -- we'll discuss this in the communication unit of the course) and the pollen-bearing stamens are placed such that the birds get the pollen all over their "faces" when probing for nectar. Thus, the birds can carry pollen to other flowers -- the plant "pays" for the efficiency and specificity of this pollination service with its nectar

Wolf and Gill's hypothesis is very simple. Sunbirds (like hummers) are very energy stressed. In fact, they can easily starve to death if prevented from feeding for a day. Thus, being in "positive energy balance" where the bird takes in more energy than it uses should be one of the bird's primary goals. Notice that while this is often assumed to be true to all animals, it certainly need not be the case in species or individuals with relatively low energy requirements coupled with good body stores of fat and/or glycogen. These animals are less well suited for tests relating territoriality to energy for the simple reason that effects may be slow to appear -- these animals, unlike sunbirds, can be said to be "energy buffered".

Wolf and Gill looked for conditions that defined when it was or was not profitable for a sunbird to hold a territory. The assumption is that energy matters so much in this species that territories should be **facultative** -- they believed that anytime the daily energy balance tips away from territoriality, a sunbird should abandon territory defense.

To construct their model, they needed a series of **energy budgets** whose values varied according to the amount of energy spent on different behaviors. Accordingly they attempted to estimate the energetic costs of the bird's main behavioral patterns:

Sitting -- the rate of energy use when a bird is alert but not moving. They got this by figuring that, based on studies of a number of birds, sitting cost about 1.5 to 2X basal rate. Incidentally, they did not measure basal rate either -- the assumed it was the same as the measured value for a closely related species (probably OK but potentially dangerous).

<u>Sleep</u>: sunbirds sleep for about 14 hours a day. Sleep is a means that in part allows them to avoid using energy. During sleep, their metabolic rates were close to what physiologists call basal. Interestingly, unlike most hummingbirds, golden sunbirds do <u>not</u> lower their body temperature and rate of metabolism (a process called "torpor") during sleep (this is a means to further reduce energy loss and therefore energy requirements).
<u>Chasing -- territorial defense</u> -- much of territorial defense in sunbirds involves flying from one place to another. Thus, they estimated the cost of flight based on equation derived for other birds and used this value for the cost of defense per time. Notice below that it is about 7.5X more costly to fly than to sit around -- this represents a huge increase in cost for a vertebrate.
<u>Foraging</u> sunbirds basically fly from one inflorescence to another. When feeding, they perch (unlike the hovering often practiced by hummingbirds). They obtained a time budget for the proportion of the time spent perched vs. flying during a feeding bout and used it, along with the estimated costs of flight and sitting, to get the cost of foraging:
<u>Flycatching</u> -- insects are the source of protein. Flycatching involves darting from a perch and seizing a flying insect. They found that little time was spent with flycatching.
Below is an example of the costs of some of these activities for golden-winged sunbirds

<u>Table 1—Power (Kcal/h) Requirements for Activities</u>

Variable	Power Requirement (Kcal/hour)
Sitting	0.400
Foraging	1.027 (~ 1.0)
Territorial defense	3.000

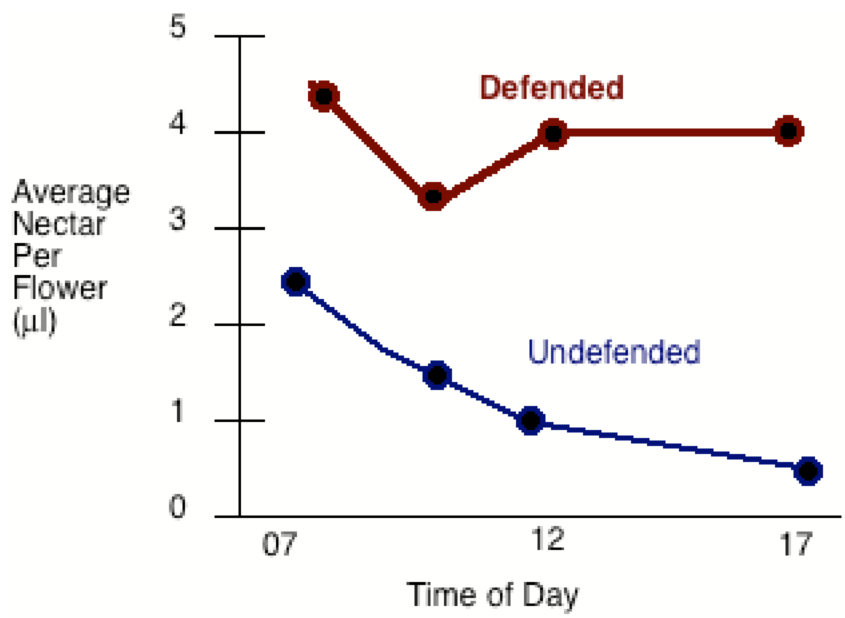
By multiplying the time spent (the **<u>time budget</u>** -- see early in the semester) in each activity by the estimated rate of energy expenditure (power) for that activity, they obtained the **cost** (energy) of each activity and the sum or all of these costs gave an estimate of the sunbird's **<u>energy budget</u>**. Here are their data for several different times of the year:

<u>Table 2 -- Energy Budgets</u>

Date	Sitting (Kcal)	Foraging (Kcal)	fly catch/ Perch change	Chasing (Kcal)	Sleeping (Kcal)	Total (Kcal)
29-30 March	2.592 (20%)	2.989 (23%)	1.140 (9%)	0.690 (5%)	5.649 (43%)	13.06
14-15 April	2.708 (22%)	2.660 (21%)	0.740 (6%)	0.915 (8%)	5.649 (45%)	12.76
19-20 April	2.880 (24%)	2.485 (20%)	0.3 (2%)	0.84 (7%)	5.649 (47%)	12.15

Notice that although the activities changed over time (reflecting differences in the availability of flowers and competitors) the total daily energy budget was very constant at about 12 to 13 Kcal per day. Thus, a sunbird MUST get this much energy daily if it is to avoid starvation (remember these are small birds with very small energy stores).

Next, they determined the amounts of nectar typically available from the flowers over a day. They obtained graphs that looked like this one:



Notice that energy was most available early in the day when flowers had not been visited. Also notice that on the average, defended flowers always contained more nectar than undefended flowers[2]. The large difference in the rate of depletion is associated with the fact that undefended flowers are visited by many different sunbirds.

Gill and Wolf also determined, by observation, the time a sunbird typically needed to visit a flower and empty it. And they also found that the sugar concentration of the host flowers (one species formed most of the sunbird's diet during the study) was constant.

Since they already knew the daily energy requirement (table 2) they could determine the amount of time that a sunbird would need to spend foraging as a function of the average amount of nectar in the flower. It was done by finding the number of flowers that needed to be visited given the flowers contained a certain average volume of nectar

[2] It was assumed that the differences in nectar had to do with defense. It is important to note, however, that it might have been possible that defended flowers were of higher quality (as noted by Gill and Wolf).

eq. 5 $$N_f = \frac{E_{requirement}}{V_{nectar/flower} * E_{energy/volume}}$$

where N_f is the number of flowers, $E_{requirement}$ is the energy requirement (energy budget), $V_{nectar/flower}$ is the average nectar volume per flower and $E_{energy/volume}$ is the amount of energy in one unit of nectar volume.

eq. 6 $$T_{forage} = N_f * t_{time/flower}$$

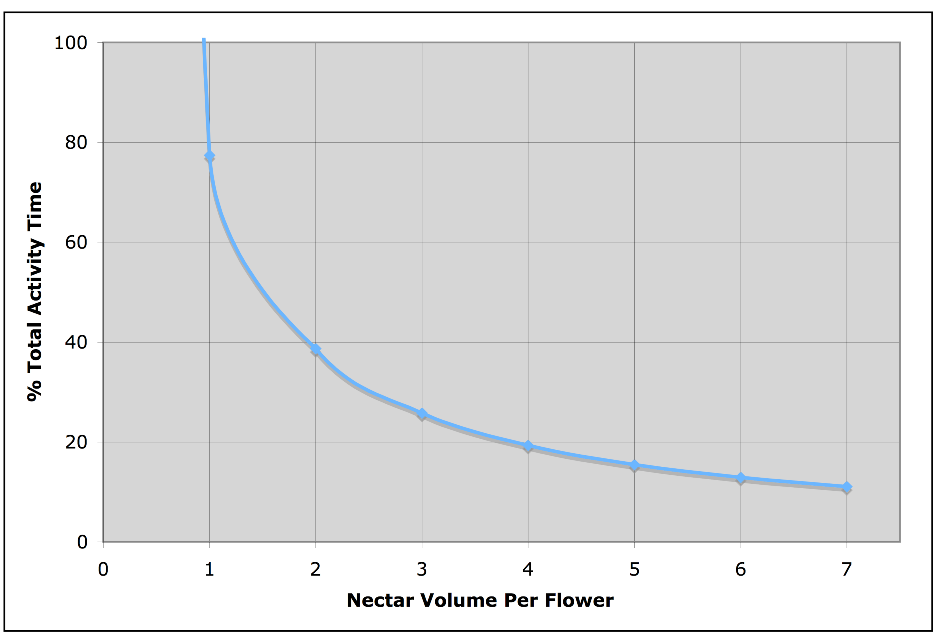
where T_{forage} is the total foraging time needed to meet the energy budget and $t_{time/glower}$ is the visit time per flower. By substituting eq. 5 into #6 we get

eq. 7 $$T_{forage} = \frac{E_{requirement}}{V_{nectar/flower} * E_{energy/volume}} * t_{time/flower}$$

When Gill and Wolf solved eq.7 for the total foraging time (which they called T_F) using field-determined values for the average time spent visiting a flower, the caloric equivalent of a volume of nectar, and the daily energy requirement of about 13 Kcal (see above), they got:

eq. 8 $$T_f = \frac{13 \text{ Kcal}}{V_{nectar} * 0.7 \frac{\text{cal}}{\mu\text{l}}} * 1.5 \text{ seconds} = \frac{7.74 \text{ hours}}{V_{nectar}}$$

The resulting plot of such an inverse function (with foraging time given as a percentage of the total daily activity time of 10 hours):



Note that at low nectar volumes it is simply impossible to get the required number of calories in 10 hours. Also notice that with increases in nectar availability, the proportion of time that must be devoted to foraging decreases rapidly at first and then slowly. The reason for the slower increase later is that the increase in nectar – say from 5 to 6 µl per flower, is proportionately a small increase (20%) as compared to say from 1 to 2 µl per flower (100% increase).

Here are some of the values as times from the previous graph. As should be obvious from equation 8, doubling the amount of nectar halves the foraging time required to obtain the minimum daily calorie requirement.

Table 3 -- Times Needed to Meet Foraging Needs

Average Volume Nectar per Flower, V_f (µl)	Time to Get Energy, t_f (hours)
1	7.74
2	3.87
3	2.58
4	1.93
6	1.29

What are the energy benefits of territories? Territories allow the owner sunbird the near-exclusive use of the flowers within the defended area. Nectar accumulates between visits and therefore the owner gets all the nectar. **Thus, the advantage of territoriality is that <u>the time required to obtain a given amount of nectar decreases</u>.**

For example, if territoriality causes allows the average payoff per flower to increase from 1 to 2 µl per day, then the bird would need to only forage 3.87 hours instead of 7.74 -- *i.e.*, there are nearly four (3.9) additional hours the bird could spend sitting which is a less expensive activity than foraging (see table 1). Likewise, if territoriality increases the yield from 2 to 3 µl, the foraging time saving is 3.87-2.58 = 1.3 hours. Notice that as the baseline nectar amount increases, the time savings in increasing one unit of nectar becomes less

However, <u>time is not our currency</u> -- <u>energy is</u>. Foraging time savings come at the energy cost of territory defense. Table 1 shows that per unit time, territorial defense is the most expensive activity! **Gill and Wolf reasoned that the <u>threshold for territoriality was where the costs associated with territorial defense (C_d) were exactly balanced by the energy savings associated with shorter foraging times</u>,** that is, the "tipping point" is where:

eq. 9 C_d = Δ Foraging Costs = Foraging Costs in Undefended-Defended

Recall that **cost of a particular activity** (in units of energy) is the **product of the power requirement for the activity and the time over which the animal engages in the activity**. Thus, we can expand eq. 9 :

eq. 10
$$C_d = (T_{f,p} * P_f) - [T_{f,r} * P_f - \Delta \text{ Sitting Costs}]$$
$$C_d = (T_{f,p} * P_f) - [T_{f,r} * P_f - (T_{f,r} - T_{f,p}) * P_s]$$

Where ***P*** refers to **power requirements** and ***T*** to **time requirements** for some activities, the subscripts ***f*** and ***s*** refer to **foraging** and **sitting** and ***p*** and ***r*** refer to **rich** (defended with high nectar content flowers) and **poor** (undefended and therefore lower nectar content) .
Notice from eq. 10 that the difference in foraging times defended (r) and non-defended habitats approximates the change in sitting time since times spent engaging in defense are, we will soon see, relatively very small. This approximation allows us to simplify eq. 10 to get:

eq. 11
$$C_{defense} = (P_f - P_s) * (T_{f,p} - T_{f,r})$$

The chart below gives the gross energy savings associated with decreased daily foraging costs. The savings are the difference between foraging costs at the lower and higher nectar levels minus the difference. The remaining columns "Net Savings Defense Levels" give the total energy savings with different amounts of territorial defense – 1% to 5% of the total daily activity time:

Avail. Nectar Vols. µl			Net Savings Defense Levels				
undefended	defended	Gross Savings	1%	2%	3%	4%	5%
1	2	2,426	2,066	1,706	1,344	986	626
2	3	806	449	89	-271	-631	-991
2	4	1,216	856	496	136	-224	-584
3	4	408	48	-312	-672	-1,032	-1,392
3	6	809	449	89	-271	-631	-991
4	6	401	41	-319	-679	-1,039	-1,399

Notice that at high defense costs and in situations where the proportional increase in nectar per flower was relatively low, defense is a losing economic option (shaded boxes).

Let's go back to modeling the cost of defense. **Recall that equation #8 allows us to estimate foraging times in golden-winged sunbirds as a function of different average nectar volumes per flower found in defended (*V_d*) and undefended (*V_u*) situations** . If we **substitute into eq. 11 specific instances of equation #8 for two different average nectar volumes** and also put in the power requirements for sitting and foraging from Table 1:

eq. 12 $$C_d = (1.027 - 0.400\ \frac{\text{Kcal}}{\text{h}}) * (\frac{7.74\ \text{h}}{V_u} - \frac{7.74\ \text{h}}{V_d})$$

a. $$C_d = 0.627\ \frac{\text{Kcal}}{\text{h}} * 7.74\text{h} * (\frac{1}{V_u} - \frac{1}{V_d})$$

eq. 13 b. $$C_d = \frac{4.853\ \text{Kcal}}{V_u} - \frac{4.853\ \text{Kcal}}{V_d}$$

c. $$\frac{1}{V_d} = \frac{1}{V_u} - \frac{C_d}{4.853\ \text{Kcal}}$$

We could plot eq. 13C as is with the average volume of nectar per flower on defended patches as the independent variable and the total cost of defense, C_d, as the independent variable. However, it is more useful to plot C_d using time units since defense time is what is actually being measured in the field. Recall that total defense cost in Kcal = Power Requirements for Defense * time. So:

a. $$\frac{1}{V_d} = \frac{1}{V_u} - \frac{P_d * T_d}{4.853\ \text{Kcal}}$$

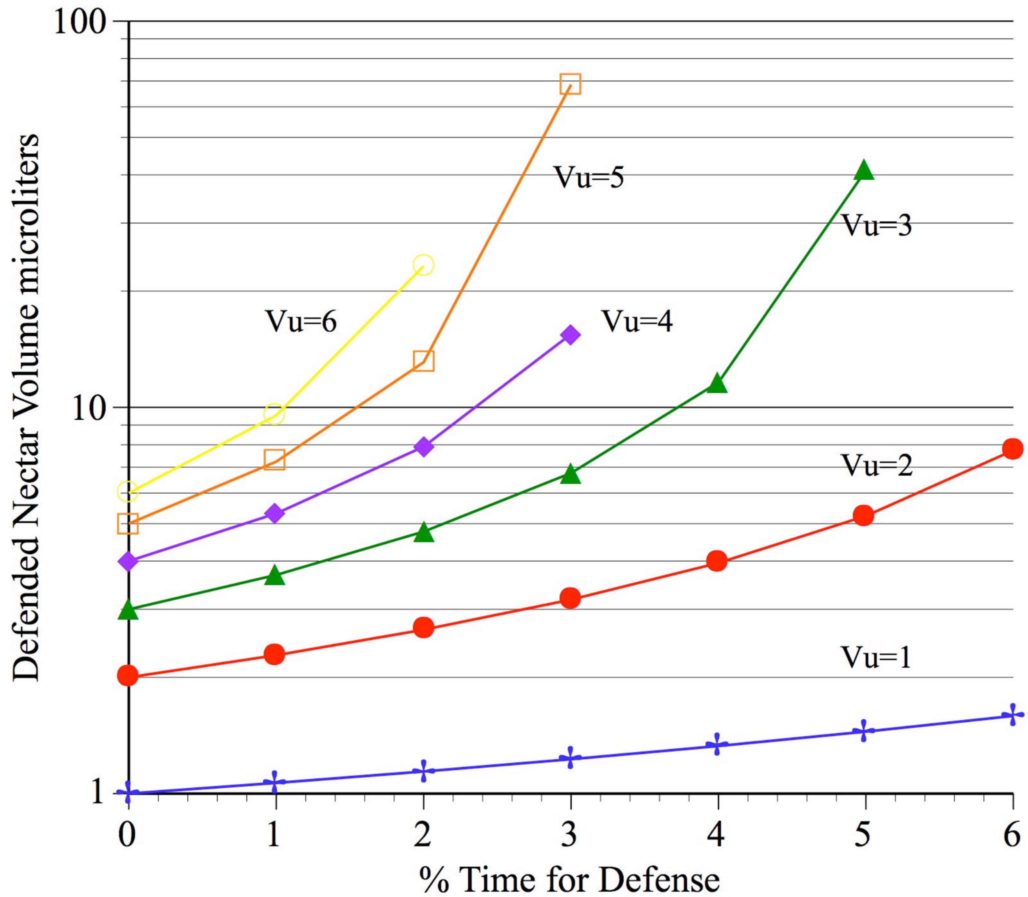
b. $$\frac{1}{V_d} = \frac{1}{V_u} - \frac{3\frac{\text{Kcal}}{\text{h}} * \frac{1\text{h}}{60\text{m}} * T_d}{4.853\ \text{Kcal}}$$

eq. 14

c. $$\frac{1}{V_d} = \frac{1}{V_u} - \frac{3\frac{\text{Kcal}}{\text{h}} * \frac{1\ \text{h}}{60\ \text{mins}} * T_d}{4.853\ \text{Kcal}}$$

d. $$\frac{1}{V_d} = \frac{1}{V_u} - \frac{0.0103}{\text{mins}} * T_d$$

Now, let's plot eq. 14d**.** The **Y-axis (dependent variable) is the average VOLUME of nectar per flower on defended patches, obtained from 14d. Our independent (X-axis) variable is defense time in minutes** and we generate a curve for each of a number of different starting volumes of nectar in flowers in undefended patches. Here are the resulting plots:



Notice that we plot the graph as V_D vs. T (given as % of daily activity time) not *1/V* vs *1/T* as in eq. 14d. This is just so that we can plot units (volume and proportion of available time) that make more intuitive sense.

Let's go over the graph on the last page:

- Each plot shows the **MINIMUM increase in nectar that MUST result from various territorial defense times in order to reach the break even point between defense and non-defense** given a certain starting (undefended) expected volume of nectar.
    - Thus, if territoriality results in an increase in nectar availability that meets or exceeds the value on the plot, then it makes good economic sense to the sunbird to become territorial.
    - Thus, if you start with an undefended volume of 2µl per flower (C_d = 0) and defend for 18 minutes per day, the average yield of nectar increases to 3 µl per flower. (see labeled point "S").
    - On the other hand, notice that it is very difficult to gain enough nectar so that flower defense makes sense if initial flower nectar levels are high.
- The separate plots are based on different initial unprotected average amount of nectar per flower (1, 2, 3, 4, and 6 µl per flower for the plots

above).

- Where each plot starts from the Y-axis the **cost of defense is zero**. Thus, the volume of nectar at these points equals the equals the "undefended" value (*i.e.*, it is the same as the value given on the right end of each plot.

What does the graphical model predict?

- **At low undefended nectar levels,** only small increases in nectar availability are required to support various levels of defense.
- On the other hand, if the initial amount of nectar is greater, then a greater amount of nectar is required to favor territoriality. In fact, it should be obvious that at high, undefended nectar levels, territorial defense never makes sense.

If the graphic model does not make total sense (and it doesn't to many when they first encounter it), perhaps another approach will help you understand the graph:. Let's determine the maximum cost of resource defense if the result is that the average nectar payoff per flower goes from 2 to 3 µl (see lowest plot on last graph).

- Recall that the break-even point for resource defense is when the energy savings obtained from less foraging time are exactly equal to the cost of defense (see discussion just prior to eq. 9).
- Now, go back and look at Table 3. You'll see that foraging times to meet daily energy requirements are 3.87 and 2.58 hours/day, respectively. Thus, the increase of 1 µl due to territoriality would result in about a 1.3 hour savings in foraging time.
- The animal can spend this time sitting instead. So, if foraging costs are about 1 Kcal/h/day and sitting costs are 0.4 Kcal/hour per day (see table 1), then:

the net energy saving = max $\boldsymbol{C_d}$ **=** savings in foraging - cost of additional sitting

max $\boldsymbol{C_d}$ **=** 1 Kcal/h/d * (1.3 h) - 0.4 Kcal/h/d * (1.3 h) = 0.78 Kcal/h/d

How much time would this "energy surplus" allow birds to spend on territorial defense? Gill and Wolf believed that he rate of energy expenditure during territorial defense is 3.0 Kcal/h (see table 1). Now, 3.0 Kcal/h is not the actual cost of territorial defense because even if the animal is not defending but is alive it, it is still using energy. So, **we need the net increment in metabolism due to territorial defense**. The simplest, but not fully justified assumption, is to assume that if not involved in defense, the sunbird is sitting[3] . Thus, the amount

[3] More realistically, one should estimate non-defense rate of metabolism on a mix of sitting and foraging.

of time a sunbird could spend defending and still make an economic go of it is:

$T_D < C_D$ / (metabolic rate during defense - metabolic rate when sitting)

For our example, C_D = 0.78 Kcal/h/d
metabolic rate during defense is 3.0 Kcal/h
metabolic rate during sitting is 0.4 Kcal/h
Thus:

$T_D <$ 0.78 Kcal/ (3.0 - 0.4 Kcal/h) = 0.3 hours or 18 minutes

How much time do sunbirds actually expend in territory defense? Gill and Wolf determined that a sunbird might expect to spend **about 17 minutes** (0.28 hours) per day defending a typical territory! **This lends support to Gill and Wolf's model -- they predicted the cutoff point was 18 minutes for the situation where territory increased the yield from 2 to 3 µl.** (note -- this model only takes economic costs of territory into account. Often, there is also a risk of injury associated with territorial defense)[4].

Just for the heck of it, let's see what happens if the original average nectar content was 4 µl and territoriality increased availability to 6 µl.
The change in foraging time is (from Table 2):
1.93-1.29=0.64 h

max $\boldsymbol{C_d}$ **=** 1 Kcal/h/d * (0.64 h) - 0.4 Kcal/h/d * 0.64 h = 0.384 Kcal/h/d

$T_D <$ 0.384 Kcal/ (3.0 - 0.4 Kcal/h) = 0.148 hours or about 9 minutes

Thus, if the nectar level was 4 in undefended flowers and increases to 6 when defended, the bird had better not spend more than 9 minutes on territory defense if it hopes to break even. Compare this with the previous case of 2 to 3 where the bird could afford to spend 18 minutes day on defense and make a go of it. If we assume that birds really do spend an average of 17 mins. a day on territorial defense, obviously a much larger increase in nectar volume would be required to make a go of it. What really happens at higher nectar availabilities is that the birds are NOT territorial. Many find this result surprising but in fact it describes the sunbird's behavior nicely.

It may seem a bit counter-intuitive that when resources are abundant that they are not defended. However, keep in mind that in such situations animals can get what they need in a short time and territoriality does not save them time nor get

[4] For example, I have observed violet saber-winged hummingbirds in Costa Rica force each other to the ground and "wrestle" and attempt to injure each other with their beaks.

them more resource since they may already have all they can use. Moreover, when there are rich resources, it is quite possible that a large number of individuals will be attracted to them. The costs of defending against so many intruders, costs will be very high and so it is probably a **far better solution to engage in scramble competition**.

VI. Territory Defense and Resource Procurement Fighting and Assessment

A. Disputes over resources often involve what are termed **escalated contests**. These typically start as inexpensive and safe affairs but they may become more serious, costly and dangerous under the right conditions.

B. A central feature of escalated conflicts is that honest communications tend to underlie them. The signals are honest because it is in both parties interest for them to be so since either party can call the other's bluff by escalating the contest from display to more serious fighting.

C. The conflicts and signals are usually highly ritualized. The benefits to both parties are that fights are avoided unless unavoidable -- fights only occur when parties incorrectly assess each other or assess each other as being essentially equal in fighting ability (and in that case, often no fight may occur if one already holds the territory or resource).

escalated and non-escalated contests

D. Example: Red Deer -- cervids -- males defend breeding areas from other males; these are also desirable patches of land. The pattern of escalation is:

1. roaring contests -- pitch, loudness , repetition and duration
2. parallel walk
3. locking of antlers and pushing
4. escalated fights with antlers where injury is a real possibility

More on this later when we discuss mating systems